

A NEW ORDOVICIAN ARTHROPOD, *SOOMASPIS*, AND THE AGNOSTID PROBLEM

by R. A. FORTEY and J. N. THERON

ABSTRACT. A new uncalcified arthropod, *Soomaspis*, is described from the latest Ordovician Soom Shale of South Africa. It is included with other primitive and uncalcified trilobites in the family Naraoiidae, the composition and evolution of which are re-evaluated. Naraoiids are considered to have arisen by the heterochronic process of hypermorphosis, whereas Agnostida, to which they bear a superficial resemblance, are progenetic. The place of *Soomaspis* and naraoiids within the trilobite-like arthropods is analysed cladistically; they comprise a sister group of the rest of the clade. The problem of classifying Agnostida is discussed in this context. Their relationships within, or outside Trilobita depend upon the methods of character analysis, and the emphasis placed on particular characters. In the analysis presented here, Agnostina comprise the sister group of Eodiscina. The inclusion of all these groups within the Trilobita is favoured.

SINCE the first description of Lower Palaeozoic fossils from the Table Mountain Group of South Africa (Cocks *et al.* 1970), continued research has elucidated the distribution and age of this unique fauna. The fossiliferous beds are confined to the Cedarberg Formation, a laterally persistent argillaceous unit (c. 120 m) among predominantly arenaceous rocks (c. 3000 m), which build up an impressive sequence of rugged mountain ranges in the southwestern Cape Province. Good exposures of the Cedarberg Formation are rare because of its recessive nature, and are seldom easily accessible. Consequently, fifteen years passed before Moore and Marchant (1981) discovered in the basal Soom Member the well-preserved trilobites described by Cocks and Fortey (1986) as *Mucronaspis*. From the trilobite and brachiopod faunas, they concluded that the age of the Soom as well as the overlying Disa Member was latest Ordovician, rather than early Silurian (Llandovery) as had been suggested by some previous authors.

Further investigation of the Soom Member resulted in the discovery of a new fauna more than 100 km north of the previous fossil sites. This fauna includes exceptionally well-preserved, giant conodont apparatuses (Theron *et al.* 1990; Aldridge and Theron 1993) sometimes preserving soft tissues of the animals, as well as eurypterids, brachiopods and orthocone nautiloids. The same fauna includes an unusual arthropod, which is the subject of this paper.

South Africa lay at high palaeolatitudes in the late Ordovician (Scotese and McKerrow 1990). The Soom Shale conformably overlies and sometimes partially interfingers with tillites of the Pakhuis Formation. It is therefore a rare example of a Palaeozoic glacio-marine depositional environment, the Soom Shale representing the outwash and fine silt fraction from the retreating ice sheet, while the fauna is indicative of open marine conditions.

The new arthropod, *Soomaspis*, is a rare fossil. It is of particular importance, however, because it is one of a group of trilobite-like animals (naraoiids) which have been claimed as related to the trilobite suborder Agnostina (which will be referred to, informally, as 'agnostids'). Some recent authors (e.g. Shergold 1991) have claimed that agnostids are not closely related to other trilobites. *Soomaspis* provides an opportunity to look again at the evidence for agnostid relationships, and to assess how naraoiids fit into the stem lineage of the Trilobita.

COMPOSITION OF NARAOIIDAE

Naraoia was originally described from the celebrated Middle Cambrian Burgess Shale of British Columbia by Walcott (1912). The type species, *N. compacta*, and a second one, *N. spiuifera* Walcott, 1931, were exhaustively revised by Whittington (1977). Because the type species has limbs preserved on many specimens, a good deal is known about its appendages, which led Whittington to make a comparison with the Trilobita, to which clade *Naraoia* was assigned as an unmineralized member. Raymond (1920) had proposed an Order Nektaspida for its reception.

Naraoia has turned out to be quite widespread. Robison (1984) reported *N. compacta* from the upper Lower to Middle Cambrian of Idaho and Utah. Zhang and Hou (1985) described new and well-preserved *Naraoia* species from Chengjiang, eastern Yunnan, China, from the Lower Cambrian. This last occurrence is particularly important because it proves that the differentiation of naraoiids from other arthropods has happened already as part of the so-called Cambrian 'explosion'. Stratigraphical evidence is therefore irrelevant for the resolution of the relationships of *Naraoia*, which must be determined by a consideration of comparative morphology using cladistic methods (Briggs *et al.* 1992; Fortey and Owens, 1990).

Here we include several more genera besides *Naraoia* in the family Naraoiidae. These are: *Liwia* Dzik and Lendzion, 1988; *Tarricoia* Hammann *et al.* 1990; *Soomaspis* gen. nov.; and *Maritiniella* Repina and Okuneva, 1969. The least fully known of these are *Liwia* and *Maritiniella*, but knowledge of the dorsal morphology of the other two is sufficient to provide a good comparison with *Naraoia*, from which they differ primarily in having freely articulated thoracic segments.

The Naraoiidae have the following characters, most of which are regarded as autapomorphies.

1. The cephalic shield is transversely oval or semicircular, and virtually without dorsal features; there are no eyes.

2. The pygidium exceeds the cephalic shield in length (sag.). This is an unusual feature in arthropods; it is only otherwise known on some undoubtedly advanced trilobites, such as Devonian Scutelluidae (e.g. Šnajdr 1981). For this reason, we regard it as a good character of phylogenetic significance. As discussed below, the large pygidium is likely to have been the result of the heterochronic process known as hypermorphosis. Hammann *et al.* (1990, fig. 5) reconstructed *Tarricoia* as having the pygidium only slightly exceeding the cephalic shield in length. Specimens from the type locality of *T. arruseusis* are all distorted in various ways and accurate assessment of proportions is accordingly difficult. A visit to the type locality by the first author and Dr L. R. M. Cocks yielded the specimen shown on Plate 1, figure 1, which apparently shows little distortion. Its pygidium is relatively longer than that in the reconstruction of Hammann *et al.*, and more like that of other naraoiids. We have introduced this modification to the proportions of *Tarricoia* in the discussions used in this paper. The character is least developed on the new genus described below.

3. Naraoiids are medium sized trilobites, commonly 20–30 mm in length; Chinese species include larger individuals. They are several times the size of the average agnostid (below).

4. There are few to no thoracic segments. The primitive state in Arthropoda is likely to have included a large number of freely articulating post-cephalic segments (Manton 1977; Briggs *et al.* 1993), and loss of such segments is generally considered to be an advanced character. On the other hand, we would attribute little systematic importance to the presence of three or four free thoracic segments in *Soomaspis*, *Liwia* and *Tarricoia*, as opposed to none in *Naraoia*. The retention of a few thoracic segments is probably a plesiomorphic character, which is not an important consideration in the placement of the group as a whole.

There are other naraoiid characters which are probably plesiomorphic. These include possession of a single pair of filiform antennae (known in *Naraoia* and *Liwia*), and the generally trilobitomorphic limb structure (*Naraoia*, see Whittington 1977). Genal spines are known in *Naraoia spinosa* Zhang and Zhou and, probably, in *N. spiuifer* Walcott also. Genal spines are a general trilobite character, and their loss in other naraoiids is a derived character, but it is not a general feature of the group.

SYSTEMATIC PALAEOLOGY

Class TRILOBITA Walch, 1771
 Order NEKTASPIDA Raymond, 1920
 Family NARAOIIDAE Walcott, 1912
 Subfamily LIWIIINAE Dzik and Lenzion, 1988
 Genus SOOMASPIS gen. nov.

Type species. Soomaspis splendida sp. nov.

Diagnosis. The diagnosis follows that of the type and only species, given below.

Soomaspis splendida sp. nov.

Plate 1, figures 2–4; Text-figure 1A–C

Type locality. Soom Shale, Keurbos Farm near Clanwilliam, Cape Province, South Africa (full locality details given in Theron *et al.*, 1990).

Holotype. Dorsal exoskeleton, showing rostral plate, Geological Survey of South Africa collection, specimen number C453.

Paratypes. Two other complete dorsal exoskeletons C405, C451; three fragmentary shields, C313, C374, C696.

Diagnosis. Naraoiid having pygidium with five segments defined by interpleural furrows. Thorax with three thoracic segments. Surface sculpture of dense pitting.

Description. The largest cephalic shield has a width of just under 20 millimetres, which suggests that the entire animal must have attained a length of at least 30 mm. Because the cuticle was unmineralized, little is preserved of the original relief. The entire exoskeleton shows signs of crushing, especially on the pygidium, and differential compaction may account for differences between the holotype and the several paratypes, with regard to such features as the clarity of pygidial segmentation and convexity of the sagittal area. Whittington (1977) inferred moderate convexity on *Naraoia compacta*, and *Soomaspis* was probably similar. However, the crushing renders measurements of proportions somewhat approximate. Cracks on the pygidium of the holotype run close to the pygidial axis, and on the exsagittal right- and left-hand side of the cephalic shield (Text-fig. 1A), which is consistent with crushing a somewhat convex median lobe. For example, the trilobite *Bienvillea* developed cracks in a comparable position when preserved in flattened mode (Fortey 1974, pl. 22, figs 9, 11).

The whole exoskeleton is about two-thirds as wide as long. Maximum width is across the cephalic shield, which is about 1.3 to 1.4 times the width of the pygidium. The pygidium slightly exceeds the cephalic shield in length, but in view of the flattening it is difficult to be precise by how much. The cephalic shield on the paratype (Text-fig. 1C) appears to preserve its anterior margin and is more than twice the sagittal length of the thorax behind it. The cephalic shield is subsemicircular to elliptical, and virtually featureless. The holotype (Text-fig. 1A), and right hand side of the specimen on Text-figure 2B, show flattened areas which are regarded as narrow posterior borders, which curve gently forwards laterally.

The holotype uniquely shows an area of cuticle lying anterior to the cephalic margin. This is not easy to interpret. To either side of, and beneath the genal regions of the same specimen there are indications of a comparatively wide doublure. This median region seems likely to represent the median part of the doublure. In this case, the lateral edges of this piece of cuticle probably represent the connective sutures; this is what would be termed the rostral plate in other trilobites. This interpretation would suggest that the holotype is a specimen which has moulted, in the course of which the cephalic shield was pushed a little backwards and the mid part of the doublure displaced forwards in the same action. If correct, this proves the cephalic doublure to be comparatively wide (sag.), as it is in *Tarricoia*. The specimen in Text-figure 1B shows a wide and ill-defined front to the cephalic shield which may be the result of crushing a similarly moulted individual.

The thorax apparently comprises three segments. It is necessary to be a little cautious about this, because the allied genera *Tarricoia* and *Livia* both have four segments. Hammann *et al.* (1990) showed that the anterior

segment in *Tarricoia* is often covered and concealed by the cephalic shield. However, the incomplete specimen on Text-figure 1C, which has the cephalic shield tipped slightly to one side, also shows three thoracic segments and no trace of a fourth. On the other hand, the specimen on Text-figure 1B apparently shows only two thoracic segments, as (undoubtedly) does the isolated thorax and pygidium (Pl. 1, fig. 3). The most likely interpretation is that there are three thoracic segments but that, as in *Tarricoia* (Hammann *et al.* 1990), the anterior segment is often concealed beneath the cephalic shield. It does not seem probable that there are two species, characterized by two or three segments respectively, because the other characters are so similar in all our material.

Each segment is a narrow, band-like strip of exoskeleton with poor indication of the axis. The specimen on Plate 1, figure 2 shows evidence of division into a broad axial region and narrow pleural regions. Pleural tips are truncate. The anterior segment on the specimen figured on Plate 1, figure 3 clearly shows the articulating half ring across the mid part of the axis. It is short (sag.), occupying about a third of the width of the axial ring. Axial rings provide good evidence for free articulation of the thoracic segments, but this movement is likely to have been limited in the dorsoventral plane as shown by the short half rings. Details of the articulation are not visible, but there is no evidence of strong ball-and-socket joints, as in advanced Trilobita. Plate 1, figure 2 shows extremely thin, depressed bands on the anterolateral margins of the segments, which fitted against the pleurae of the segment in front.

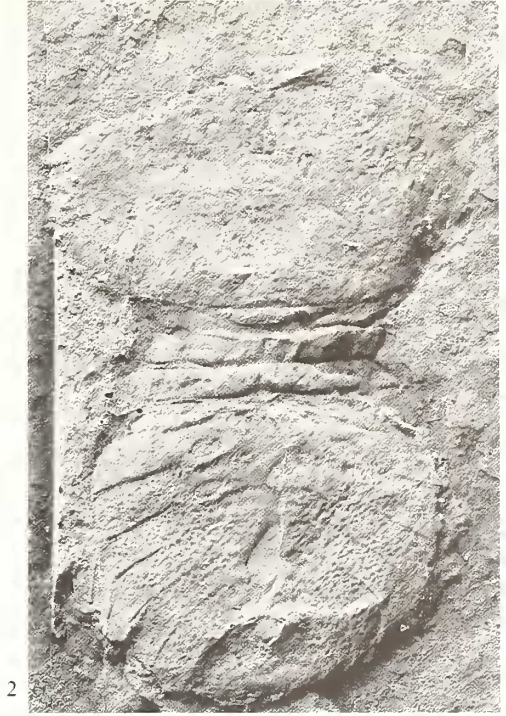
The pygidium is just wider than long. There is a striking difference between the two best specimens (Pl. 1, figs 2–3). The larger has a prominent elevated median band which is not evident on the smaller. The latter specimen shows additional details on the axial region. However, the crack running sagittally on this specimen may have served to reduce the prominence of any ridge. A median ridge is present also on other complete specimens of *Soomaspis*, and also the pygidium of *Tarricoia*. It is unlikely that the median ridge is the trace of the soft gut impressed on the dorsal surface. If it were filled with sediment, one might expect to see signs of the cuticle draping around such a structure as it decayed, for which there is no evidence. It is considered more likely to have been an original structure, as in *Tarricoia*, possibly exaggerated by flattening. Pleural fields include five segments bounded by distinct furrows which are present on the outer parts only of the pleural fields. The posterior ends of the interpleural furrows curve backwards into spine-like terminations, but these do not apparently project beyond the pygidial margin. Where the furrows stop adaxially, this delimits the axial region, which therefore takes up more than one-third of the pygidial width anteriorly. Such an interpretation is supported by the presence of muscle scars on the outer edge of this region (Pl. 1, fig. 2), shown by one specimen. Three such pairs are clearly shown, each lying close to a segmental boundary, and transversely elliptical in outline. Presumably similar muscle attachment areas were related to posterior segments also, but their trace is obscure. The specimen on Plate 1, figure 3 (left hand side) in particular shows an anterior pygidial border, which appears to extend farther adaxially than the inferred width of the axis. The same specimen shows the narrow doublure (right hand side), which narrows farther backwards. The dorsal surface of the pygidium certainly, and the mid-part of cephalon probably, is covered with rather coarse pits (Pl. 1, fig. 4).

Discussion. The type and only known species of *Soomaspis* can be compared with those nektaspidi with thoracic segments. The closest stratigraphically is *Tarricoia arrusensis* Hammann *et al.*, 1990, from the Ordovician 'Puddinga' sequence of Sardinia. *Tarricoia* has four thoracic segments, and the pygidium is entirely without dorsal segmentation (Pl. 1, fig. 1). *Tegopelte gigas* Simonetta and Della Cave, 1975, from the Middle Cambrian Burgess Shale has three thoracic divisions according to Whittington (1985). This is a very large arthropod, of which the dorsal side is poorly known. Whittington showed that the three thoracic divisions, which are unusually long (sag.), included several limb pairs per division, which is unique. *Tegopelte* is also thought to have had eyes inserted

EXPLANATION OF PLATE I

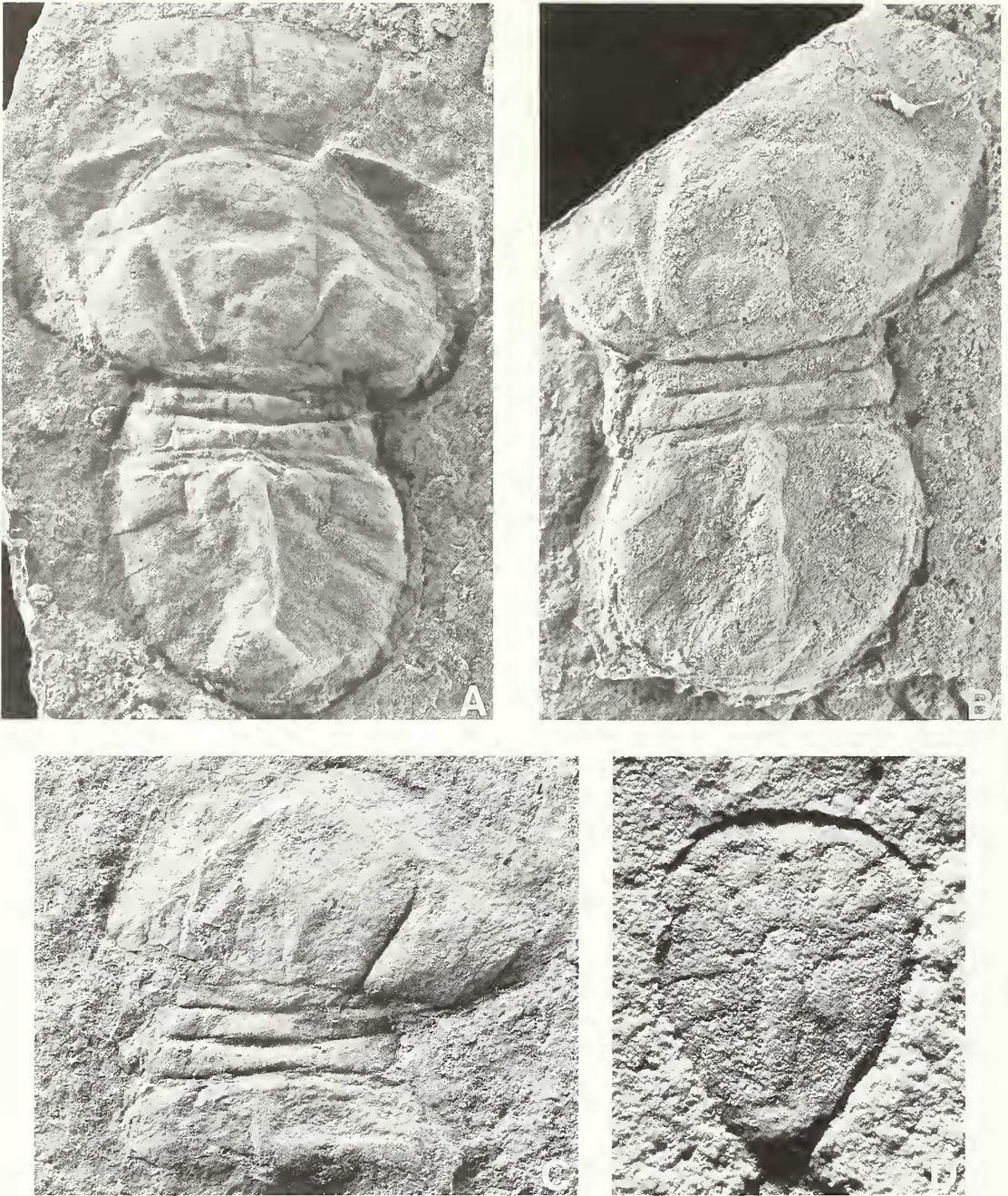
Fig. 1. *Tarricoia arrusensis* Hammann *et al.* Natural History Museum, It 21084; type locality, near Fluminimaggiore, southwest Sardinia; 'Puddinga' Formation (Ordovician); $\times 4$.

Figs 2–4. *Soomaspis splendida* gen. et sp. nov. Paratypes; Keurbos farm, near Clanwilliam, South Africa; Soom Shale (Ordovician). 2, Geological Survey of South Africa, specimen C405; latex cast from external mould of entire dorsal shield showing pygidial musculature; $\times 7.5$. 3–4, Geological Survey of South Africa, specimen C313; pygidium and two thoracic segments; 3, internal mould showing doublure; $\times 8$; 4, detail of external mould showing anterior border furrow; $\times 10$.



4

3



TEXT-FIG. 1. A–C, *Soomaspis splendida* gen. et sp. nov.; specimens stored at the Geological Survey of South Africa; Keurbos farm, near Clanwilliam, South Africa; Soom Shale (Ordovician). A, C453; latex cast of holotype, with doublure; $\times 5$. B, C451; latex cast of paratype; poor anterior definition of cephalic shield may be due to conflation with doublure; $\times 5$. C, C374; internal mould of incomplete larger specimen showing three thoracic segments; $\times 4$. D, giant protaspis cautiously attributed to *Naraoia* by Hou *et al.* (1991); Nanjing Institute of Geology and Palaeontology, specimen I15282 (photograph kindly supplied by Dr J. Bergström); Chenjiang fauna, China; Lower Cambrian; $\times 16$.

on the cephalic shield. We agree with Whittington's assessment that its trilobite status is uncertain. *Maritimella* Repina and Okuneva (Middle-Upper Cambrian, Far-eastern Russia) presents another problem, in that it looks, superficially at least, much like *Naraoia*, but is described as having dorsal eyes and 'convexities' on the 'opisthosoma' (? = pygidium). The question is, perhaps, its distinction or not from *Naraoia*, and it will not be discussed further here.

The genus *Livia* was described from basal Cambrian claystones from Poland (see Dzik and Lendzion 1988). Like *Tegopelte*, it is imperfectly known, but it does provide the closest comparison with *Soomaspis*. The presence of antennae on *Livia* is of no significance, because they are symplesiomorphic for Trilobita (and indeed Arthropoda). *Livia* had four thoracic segments, and the relatively narrow axis is strongly defined on the dorsal surface of the pygidium of *L. convexa*. *Livia convexa* may well be anonymous with *L. plana* from the same horizon (*vide* Dzik and Lendzion 1988, p. 35), which is known from articulated material. Whether or not this is the case, *Livia* has free spines on the pygidial margin, and the segmental boundaries are not defined on the pleural fields of the pygidium, as they are in *Soomaspis*. The spines on the pygidium of *Livia* are probably homologous with the segmental boundaries on *Soomaspis*. There are five pairs on the former which may indicate a similar segmental number to *Soomaspis*, if they were developed on each segment. Whittington (1977) described seven pairs of marginal spines on *Naraoia spinifera* Walcott from the Burgess Shale. Considering that they are stratigraphically so far apart, *Soomaspis* and *Livia* are remarkably similar. The differences in the thorax and pygidium are considered enough to separate them at generic level, although this judgement could be modified when more is known of *Livia*.

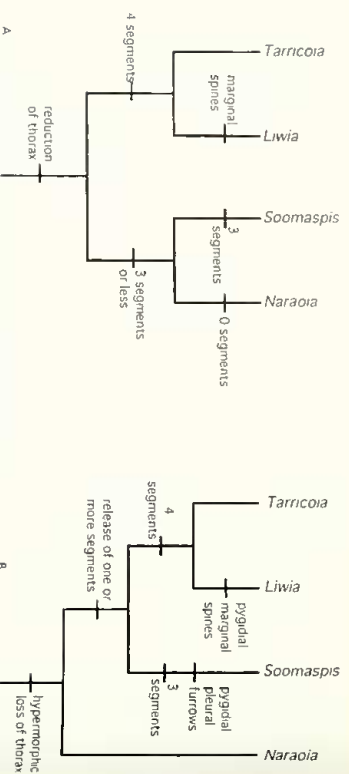
RELATIONSHIPS WITHIN NARAOIIDAE

It is possible to make suggestions as to the relationships between the naraoiid genera (Text-fig. 2). Because there are so few characters, however, these relationships are open to more than one interpretation, and the morphology-based tree differs from that based on stratigraphy. For this level of analysis, no particular purpose is served in using computer based phylogenetic programmes such as PAUP. It is generally thought that the presence of free thoracic segments is the more primitive condition in arthropods (e.g. Hessler and Newman 1975; Briggs and Fortey 1989). If this is the case, then *Naraoia*, in which there are no free segments, is more derived than other naraoiids considered here. This interpretation would suppose that, as in all trilobites, release of thoracic segments occurred from the forward edge of the pygidium (Whittington 1959). This process is suppressed in *Naraoia*. Such an evolutionary scenario makes sense, because the dimensions of pygidium-plus-thorax in relation to the cephalic shield in *Soomaspis* comes close to that of pygidium to cephalon in such *Naraoia* species as *N. spinosa* (Zhang and Hou 1985, pl. 4, fig. 1); in other words, the *Naraoia* pygidium might 'contain' the thorax (Briggs and Fortey 1992, p. 366), which is expressed in *Soomaspis* other liwiines. If this thoracic reduction is accepted as an important advanced character then the cladogram shown on Text-fig. 2A summarizes the relationships between genera.

It should be noted that the branching order in this tree bears no relationship to the stratigraphical order of appearance of the genera; if anything, rather the reverse, because the four-segmented *Tarricoia* is stratigraphically young.

To bring the inferred relationships more in line with stratigraphical order, we have to make an opposite assumption about the genesis of the thoracic segments. This assumption is that the no-segment condition of *Naraoia* was attained at a single mutation by a process of hypermorphosis (see below) of the larval state – equivalent to becoming a huge degree 0 meraspis. Then the release of free segments becomes instead a derived condition – a reversal of what would otherwise be considered the normal character polarity. This results in the hypothesis of relationships shown in the cladogram (Text-fig. 2B). This version has the appeal that the youngest genus (*Soomaspis*) is also that with the best expressed post-cephalic segmentation, notably the only one in which the pygidial pleural fields show clear intersegmental boundaries.

In the context of general arthropod phylogeny, the cladogram on Text-figure 2A is the more acceptable, particularly if parsimony is the arbiter as is usual in cladistic methods. The character

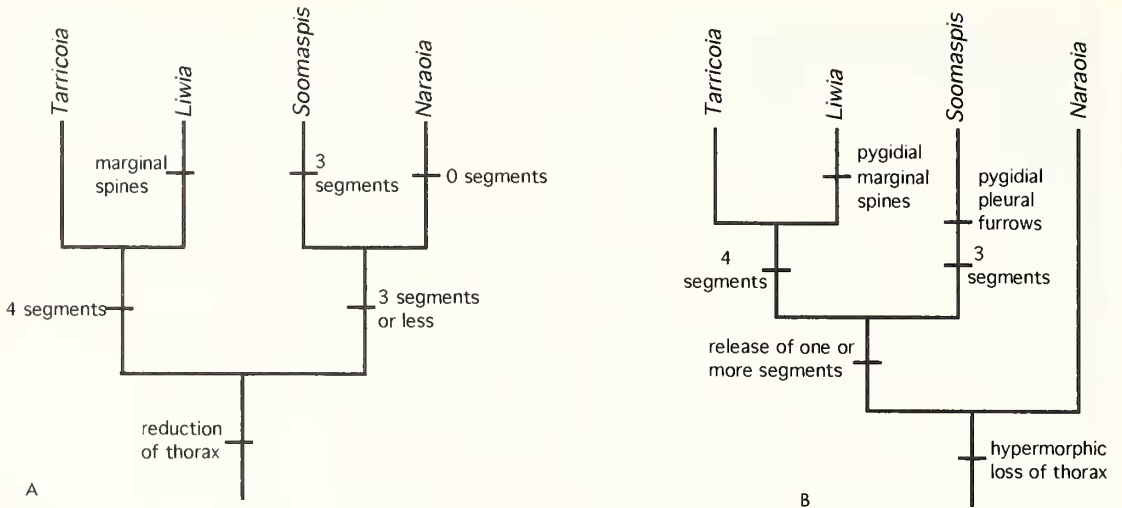


TEXT-FIG. 2 Two hypotheses of relationships between genera within Naraoiidae as understood here. A, assumes more thoracic segments are primitive. B, assumes that the condition in *Naraoia* was primitive, and release of thoracic segments progressive.

polarity 'reversals' involved with the alternative Text-fig. 2a) are difficult to prove. The occurrence of *Liwia*, with four free segments, early in the Cambrian, rather reduces the force of the stratigraphical argument, although it remains true that *Naraoia* is far more widely known in Cambrian strata. With rather few characters, and rare occurrences of fossils, one should perhaps be cautious about reading too much into stratigraphical sequence. However, it will be interesting to see whether further naraoiids are discovered at other stratigraphical levels, for example in the later Cambrian or early Ordovician, which are more consistent with placing *Naraoia* as the sister group of advanced naraoiids rather than a genus with free thoracic segments. As to function, D. E. G. Briggs has observed (written communication, 1994) that a fused carapace would have served as a support for the massive gnathobases which *Naraoia* is known to have possessed.

HETEROCHRONIC PROCESSES IN THE ORIGIN OF NARAOIIDS AND AGNOSTIDS

The importance of heterochronic processes in generating new morphologies in Cambrian trilobites has been demonstrated by McNamara (1978, 1981). Both naraoiids and agnostids have few thoracic segments and large pygidia, which suggests that pedomorphic processes, in the broad sense, may plausibly account for their peculiar characteristics. This idea has been in currency for a very long time. For example, Salter (1873, p. 48) remarked of *Agnostus minutus* that 'it represents well the embryonic forms of larger trilobites'. What Salter implied was that the release of segments during normal trilobite ontogeny was somehow 'arrested' at an early stage in agnostoids. A more refined classification of heterochronic processes (Gould 1977, summarized in McKinney and McNamara 1991) has permitted critical scrutiny of the timing of developmental shifts. Such changes may be important in rapid appearance of new *hampshire*, not least because a single change at a gene which operates developmental timing may effect profound changes in morphology without the evolution of new, complex organs. Such changes operate upon what is already implicit in the genome. In the discussion which follows, we have used the size of descendant adult as a proxy for time, because we do not have independent evidence for maturation times in trilobites. This seems reasonable given the striking size differences in the trilobites under comparison.



TEXT-FIG. 2. Two hypotheses of relationships between genera within Naraoiidae as understood here. A, assumes more thoracic segments are primitive. B, assumes that the condition in *Naraoia* was primitive, and release of thoracic segments progressive.

polarity 'reversals' involved with the alternative (Text-fig. 2B) are difficult to prove. The occurrence of *Liwia*, with four free segments, early in the Cambrian, rather reduces the force of the stratigraphical argument, although it remains true that *Naraoia* is far more widely known in Cambrian strata. With rather few characters, and rare occurrences of fossils, one should perhaps be cautious about reading too much into stratigraphical sequence. However, it will be interesting to see whether further naraoiids are discovered at other stratigraphical levels, for example in the later Cambrian or early Ordovician, which are more consistent with placing *Naraoia* as the sister group of advanced naraoiids rather than a genus with free thoracic segments. As to function, D. E. G. Briggs has observed (written communication, 1994) that a fused carapace would have served as a support for the massive gnathobases which *Naraoia* is known to have possessed.

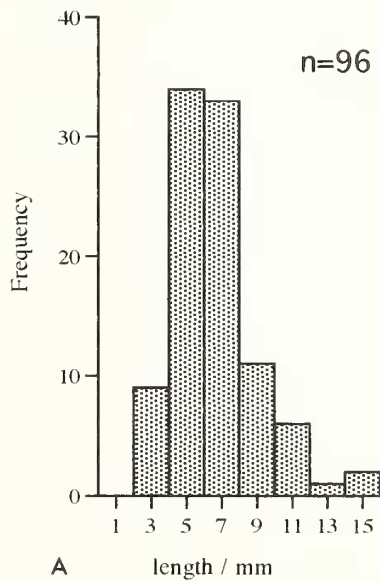
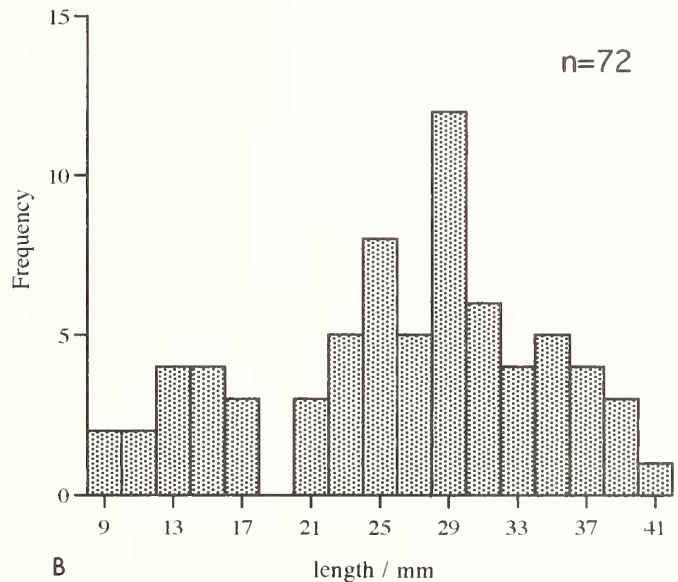
HETEROCHRONIC PROCESSES IN THE ORIGIN OF NARAOIIDS AND AGNOSTIDS

The importance of heterochronic processes in generating new morphologies in Cambrian trilobites has been demonstrated by McNamara (1978, 1981). Both naraoiids and agnostids have few thoracic segments and large pygidia, which suggests that pedomorphic processes, in the broad sense, may plausibly account for their peculiar characteristics. This idea has been in currency for a very long time. For example, Salter (1873, p. 48) remarked of '*Agnostus trinodus*' that 'it represents well the embryonic forms of larger trilobites'. What Salter implied was that the release of segments during normal trilobite ontogeny was somehow 'arrested' at an early stage in agnostoids. A more refined classification of heterochronic processes (Gould 1977; summarized in McKinney and McNamara 1991) has permitted critical scrutiny of the timing of developmental shifts. Such changes may be important in rapid appearance of new *baupläne*, not least because a single change at a gene which operates developmental timing may effect profound changes in morphology without the evolution of new, complex organs. Such changes operate upon what is already implicit in the genome. In the discussion which follows, we have used the size of descendent adult as a proxy for time, because we do not have independent evidence for maturation times in trilobites. This seems reasonable given the striking size differences in the trilobites under comparison.

Agnostids

Agnostids are invariably small. A figure for the average length of the agnostid dorsal exoskeleton has been calculated using the most comprehensive recent monograph featuring well-preserved examples from the mid-Cambrian acme of the group (Öpik 1979). This work figures some ninety-six articulated specimens, distributed amongst almost as many species, which are well enough preserved to give a measure of dorsal exoskeletal length. Specimens referred to by Öpik as 'immature' are excluded. If anything, this will bias on the large side, because authors naturally tend to choose larger specimens for illustration. The average length is 6.7 mm, and 90 per cent of specimens fall between 5 mm and 10 mm. The largest figured specimen in Öpik's work is 17 mm. One can find larger agnostids, especially among the smooth taxa. The largest known agnostid may be '*Phalacroma glandiforme* (Angelin); an entire specimen illustrated by Westergaard (1946, p. 15, fig. 13) is 20 mm long, and a cephalon (Westergaard 1946, p. 15, fig. 6) indicates that this species may have grown even larger. However, these are most exceptional among Agnostina, on the 'tail' of the upside of a normal distribution curve (Text-fig. 3), and most species are 10 mm or less. Nor

agnostids

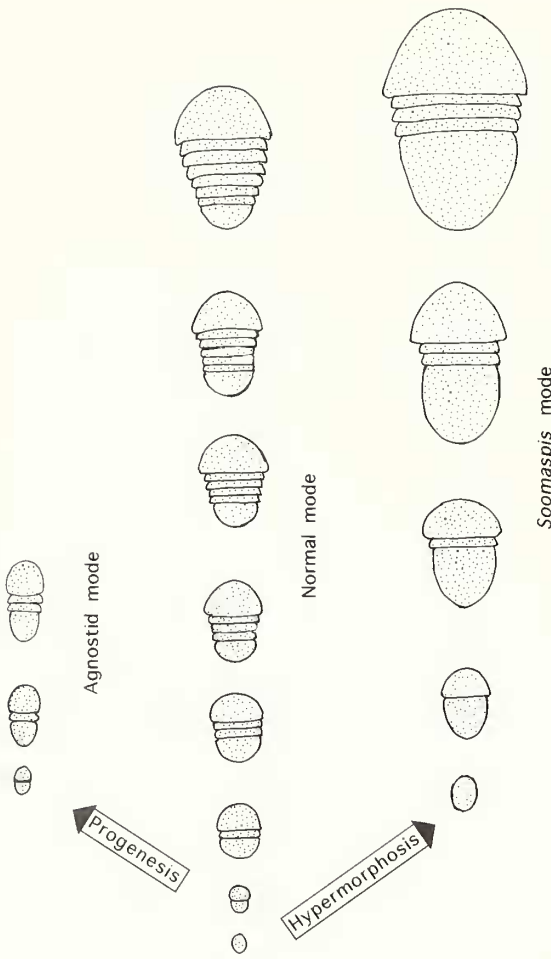
*Naraoia*

TEXT-FIG. 3. Size frequency histograms. A, trilobites of the suborder Agnostina, based on complete trilobites of broadly comparable age illustrated by Öpik (1979), B, *Naraoia*, based on Whittington (1977).

is there any obvious trend towards size increase with time, because the youngest Ordovician agnostid, *Arthrorhachis tarda* (Barrande), does not attain any greater length than its Cambrian relatives.

This indicates that the agnostids are, in terms of heterochronic development, *progenetic* (Briggs and Fortey 1992, p. 348). They are like several other well-known trilobites, *Shumardia* and *Schmalensecia* perhaps being the classic examples (McNamara 1983; Fortey and Rushton 1980), in which reproductive maturity has been achieved relatively earlier than in the ancestor, usually at a smaller size. This is a precocious onset of the maturation process relative to the ontogenetic

TEXT-FIG. 4. Different heterochronic origins of agnostids and naraoiids (exemplified by *Soomaspis*), the former progenetic, the latter hypermorphic, as compared with a simplified ontogenetic trajectory of 'normal' trilobite type.



trajectory. Agnostids were probably able to reproduce at smaller size than most trilobites, which may have had advantages for organisms which have been claimed as part of the Early Palaeozoic plankton (Robison 1972).

Once this heterochronic change was attained it apparently could not be reversed. The developmental pathway was 'committed' (Reidl 1978). Hence the small size of agnostids is not only because natural selection acted to keep them small; it is also a product of the phylogenetic history of the group, which is progenetic.

Naraoiids

Naraoiids differ from the agnostids in that their size is no different from that of a 'normal' trilobite. Whittington's (1977, text-fig. 2) measurements provide quantitative data on the length of *Naraoia* which can be compared with the agnostoid data herein (see Text-fig. 3). He showed a normal curve with a peak at 30 mm, and a maximum size a little over 40 mm. Zhang and Hou's (1985, pl. 1, fig. 1) Lower Cambrian naraoiid from China is also 40 mm long. Allowing for distortion, specimens of *Tarricoia* are commonly about 30 mm long; *Soomaspis* are mostly about 20 mm long. In short, the size of mature naraoiids begins at the dimensions at which agnostids end, and at four or five times their average size.

This size difference is more than trivial, because it is likely to result from the operation of a different heterochronic mechanism. What has happened in the naraoiids is that the larval growth trajectory has *increased* in size, so that the adult morphology shares larval characteristics by virtue of their being displaced into large individuals. This is the process described as *hypermorphosis*. Although this results in mature individuals with 'larval' characteristics, as in the agnostoids, the kinetics of the process is entirely different from the one pertaining in that group (Text-fig. 4). As we have seen, the one cannot and does not change into the other, because the developmental pathways are fixed once the ancestral condition has been lost. The kinetics of hypermorphosis and progenesis are opposite, but this has not prevented confusion between the different, broadly paedomorphic mechanisms, as McKinney and McNamara (1991) have described.

The interpretation of naraoiid phylogeny makes some difference to the way one interprets this hypermorphosis. If *Naraoia* itself is taken as the first naraoiid (as in Text-fig. 2B), then the degree of hypermorphosis is prodigious: essentially, *Naraoia* is a massively inflated 'degree 0' meraspis. It is interesting to note in this connection Hou *et al.*'s (1991) description of an enormous protaspis (see Text-fig. 1D) from the Lower Cambrian of China, which they attributed to *Naraoia*. This is what would be expected under a hypermorphic hypothesis. The hypermorphosis necessary if *Soomaspis* or *Tarricoia* are considered to be the primitive member of the clade is less, but still considerable, because degree 3 or degree 4 meraspidites of other trilobites are only a few millimetres long, at most (Whittington 1959).

Homologies between agnostids and naraoiids

The further implication of such different origins for naraoiids and agnostids is to call into question assumptions about the status of characters which could be claimed as homologies between these two groups. At first glance, the general resemblance between agnostoids and naraoiids is compelling, especially if *Tarricoia* and *Soomaspis* are incorporated into the family as we advocate. However, if their heterochronic origin is different, it is possible that shared resemblances are, after all, homoplasies.

The case of blindness will serve as an example. Both Agnostina (Agnostidae, etc.) and Naraoiidae are blind. Blindness in arthropods is secondary, not primitive, and therefore loss of eyes is a potential synapomorphy of a clade. However, if Eodiscina are related to Agnostina, this group includes species *with* well developed dorsal eyes. But this group is also progenetic (small size, few segments, etc.), and plesiomorphic in other characters, which provides both a developmental link with the Agnostina and evidence that eye loss in the progenetic line (Agnostina) is possibly separate from that in the hypermorphic line (naraoiids).

THE AGNOSTID PROBLEM

Trilobites of the suborder Agnostina are common and varied fossils in Cambrian and Ordovician rocks. Their relationship to more conventional trilobites has always been controversial, and continues to be so. The problem centres upon whether they are trilobites at all, or constitute a distantly related group with a 'separate' ancestry. Allied to this is the question whether typical agnostids (Agnostina, with some ten families according to Shergold *et al.* 1990) are or are not related to Eodiscina, a group which is not disputed as belonging to the Trilobita. Naraoiids come into the argument because they resemble agnostids sufficiently to be regarded as the possible sister group of agnostids and other trilobites (Ramsköld and Edgecombe 1991).

It is not in question that Agnostina were highly specialized arthropods, with a whole series of autapomorphies. This has become particularly clear since the description of the appendages of *Agnostus pisiformis* by Müller and Walossek (1987). For example, the limbs of this agnostid are more individually specialized than in known typical trilobites, and the exites in particular are somewhat reduced. Of exoskeletal structures, the agnostid thorax is peculiar and unique, both with regard to articulation and in losing the first thoracic half-ring, which produces a cephalothoracic

aperture during enrollment. No example of an agnostid protaspis has been discovered, although 'degree 0' meraspides are well-known, which implies an idiosyncrasy in its development. However, impressive though these differences are, they do not solve the problem of agnostid relationships, which have to be based on an evaluation of characters which agnostids *share* with other arthropods. After all, it is possible that these peculiarities were largely adaptations for their undoubted specializations, whether these were for planktonic life (Robison 1972), or as ectoparasites (Bergström 1973), or as ostracode-like epibenthos (Pek 1972). In the same way, living copepods and ostracodes are diminutive arthropods with many individual peculiarities, but their relationships within the phylum are determined by the crustacean homologies they share with more conventional relatives.

The three main hypotheses concerning the agnostid problem may be summarized as follows.

1. Agnostids are *not* trilobites. Their resemblance to eodiscines is a matter of convergence (Shergold 1991; Ramsköld and Edgecombe 1991, text-fig. 1). True trilobites include the eodiscines, which were derived from some ptychoparioid ancestor. This view of agnostids has had a long tradition among North American palaeontologists, for example, as stated by Resser (1938, p. 47), 'This group of Crustacea... a subclass parallel to the Trilobita'. Recently, some workers of this persuasion have favoured a more open verdict on the origin of agnostids, preferring to invoke some unknown (presumably Precambrian) ancestor (Shergold 1991; Walossek and Müller 1990). Ramsköld and Edgecombe (1991) portrayed the agnostids as a sister group of restricted Trilobita.

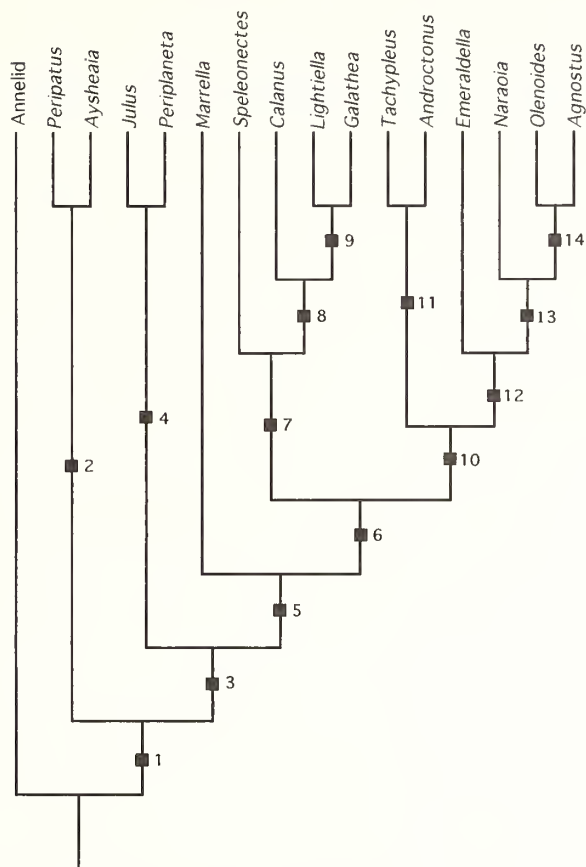
2. Agnostids *are* trilobites, and Eodiscina are their sister group. This clade is more closely related to other trilobites than to naraoiids. This view is implicitly that adopted in the *Treatise on Invertebrate Paleontology*, and was explicitly examined by Fortey (1990). Fortey analysed the problem cladistically, and found more characters supporting a clade Agnostina-plus-Eodiscina, than assuming separate origins for these groups. He placed this clade within Trilobita above olenelloids. Fortey and Whittington (1989) and Ramsköld and Edgecombe (1991) concurred that olenelloids were trilobites, *contra* Lauterbach (1983).

3. Agnostids *are* trilobites, and were derived from more than one eodiscoid group. This view was expressed most recently by Zhang *et al.* (1980, text-fig. 7); it would render the Agnostina polyphyletic. This view does not require further discussion here because, if it were true, nobody disputes that eodiscids (and hence agnostids) are trilobites. However, it does seem that the long list of agnostid autapomorphies (e.g. Fortey 1990; Müller and Walossek 1987) makes it probable that they are a monophyletic group.

Character analysis is the correct way to resolve these competing hypotheses, but this is not as simple as it may seem, because not all the relevant fossils have full information available; for example, limbs are not known for all the groups, e.g. eodiscoids. Character analysis of the taxa for which only hard parts are available does not necessarily yield the same result as those for which complete skeletal information is known.

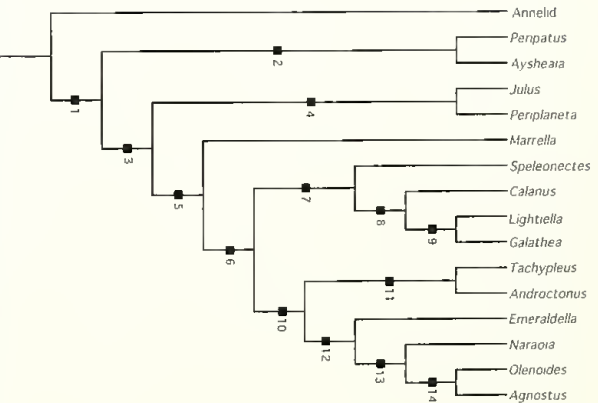
Whole organism approach to the agnostid problem

Using examples of taxa for which limbs have been described generates a large character matrix for which parsimony methods of cladistic analysis (such as PAUP) are appropriate. Several attempts to place agnostids within the arthropods as a whole have been attempted, using progressively refined character definitions (Briggs and Fortey 1989; Briggs, Fortey and Wills 1992; Wills, Briggs and Fortey 1994). These cladistic analyses included agnostids as one of more than forty arthropods, including both Burgess Shale species and primitive members of extant groups, for which the coding of many homologous skeletal and appendage characters was practicable. All the most parsimonious trees from all the analyses included agnostids together with naraoiids and higher trilobites (represented by *Olenoides*) in the same clade. This clade could be termed Trilobita. In this sense, trilobites occupied a rather advanced position on all trees, comprising a sister group to limuloids and other Arachnida, while crustaceans and crustacean-like arthropods resolved at lower nodes. A simplified version of this analysis is shown in Text-figure 5, a unique solution with the taxa chosen,



TEXT-FIG. 5. Cladogram of trilobites and selected arthropods belonging to other major groups, based on coding of characters of whole organism (full data given in Wills *et al.* 1994), including limbs. *Naraolia* is the sister group of other trilobites, including *Agnostus*. Synapomorphies listed below are not coded individually, but are summarized for each branch. 1, Inner rami of trunk appendages present. 2, Inner rami of appendages of second post-acronal somite present; inner rami of trunk appendages with a terminal group of claw-like reflexed spines; terminal trunk division with appendages. 3, Cuticle sclerotized; labrum present; increase from one to five post-acronal somites incorporated into the cephalon; trunk appendages sclerotized and stenopodous. 4, Compound eyes present; appendages of third post-acronal somite modified as mandibles biting with their tips; tracheae present. 5, Cephalic shield entire or as a single unit followed by a variable number of associated tergites; presence of a doublure; inner rami of appendages of second post-acronal somite present; outer rami of trunk appendages present. 6, Appendages of third post-acronal somite with gnathobases. 7, Outer rami of appendages of second post-acronal somite present; appendages of third post-acronal somite modified as gnathobasic mandibles; terminal trunk division with appendages. 8, Appendages of second post-acronal somite antenniform; filaments absent from the outer rami of trunk appendages. 9, Post-cephalic articulation with overlapping pleurae; differentiation of an abdomen; trunk appendages with distinctive epipodites; gut diverticulae present. 10, Increase from five to six post-acronal somites incorporated into the cephalon; outer rami of trunk appendages unsegmented. 11, Median eye present; appendages of first post-acronal somite modified as chelicerae; appendages of second post-acronal somite modified as pedipalps; anus ventral in the penultimate division of the body; terminal body division styliform. 12, Post-cephalic articulation with overlapping pleurae; inner rami of trunk appendages spinose; trunk appendages with gnathobases or protopodal endites; outer rami of trunk appendages with distal lobe. 13, Trilobation; marginal rim present; pygidium present; reduction from six to four post-acronal somites incorporated into the cephalon; outer rami of appendages of second post-acronal somite present; anus ventral in the terminal division of the body; gut diverticulae present. 14, Cuticle mineralized with calcium carbonate; genal spines present; differentiation of an abdomen.





TEXT-FIG. 5. Cladogram of trilobites and selected arthropods belonging to other major groups, based on coding of characters of whole organism (full data given in Wills *et al.* 1994), including limbs. *Naraoia* is the sister group of other trilobites, including *Agnostus*. Synapomorphies listed below are not coded individually, but are summarized for each branch. 1. Inner ramus of trunk; appendages present. 2. Inner ramus of appendages of second post-axonal somite present; inner ramus of trunk; appendages with a terminal group of claw-like reflexed spines; terminal trunk division with appendages. 3. Cuticle sclerotized; labrum present; increase from one to five post-axonal somites incorporated into the cephalon; trunk appendages sclerotized and stenopodous. 4. Compound eyes present; appendages of third post-axonal somite modified as mandibles birng with their tips; tracheae present. 5. Cephalic shield entire or as a single unit followed by a variable number of associated tergites; presence of a double; inner ramus of appendages of second post-axonal somite present; outer ramus of trunk; appendages present. 6. Appendages of third post-axonal somite with gnathobases. 7. Outer ramus of appendages of second post-axonal somite present; appendages of third post-axonal somite modified as gnathobasic mandibles; terminal trunk division with appendages. 8. Appendages of second post-axonal somite antenulariform, filaments absent from the outer ramus of trunk; appendages. 9. Post-cephalic articulation with overlapping pleurae; differentiation of an abdomen; trunk appendages with distinctive epipodites; gut diverticulae present. 10. Increase from five to six post-axonal somites incorporated into the cephalon; outer ramus of trunk; appendages unsegmented. 11. Median eye present; appendages of first post-axonal somite modified as chelicerae; appendages of second post-axonal somite modified as pedipalps; anus ventral in the penultimate division of the body; terminal body division styliform. 12. Post-cephalic articulation with overlapping pleurae; inner ramus of trunk; appendages; spines; trunk appendages with gnathobases or protopodal endites; outer ramus of trunk; appendages with distal lobe. 13. Triabation; marginal rim present; Pygidium present; reduction from six to four post-axonal somites incorporated into the cephalon; outer ramus of appendages of second post-axonal somite present; anus ventral in the terminal division of the body; gut diverticulae present. 14. Cuticle mineralized with calcium carbonate; genital spines present; differentiation of an abdomen.

TABLE 1. List of characters of exoskeleton used to produce cladistic analyses on Text-figures 7 and 8. Note that the coding on character 17 is changed as shown in square brackets to produce the coding for Text-figure 8.

-
- 1 Glabella: defined dorsally (1), not defined dorsally (0).
 - 2 Few thoracic segments – by progenesis (1), by hypermorphosis (2). Normal number of thoracic segments (0).
 - 3 Thoracic articulation: trilobite style (1), agnostoid style (2), poorly developed articulation (0).
 - 4 Doublure on cephalon: wide (0), narrow, reduced (1).
 - 5 Hypostome: present (1), absent (0).
 - 6 Hypostome condition: natant (1), conterminant (0). Note: the homology of hypostome and the labrum in *Tachypleus* is dubious and the coding given for the latter in Table 2 is a default coding.
 - 7 Cuticular terrace ridges on venter: present (1), absent (0).
 - 8 Calcified protaspis: present (1), absent or unknown (0).
 - 9 Pygidium: present (1), absent (0).
 - 10 Dorsal eyes: present (0), absent (1).
 - 11 Calcified cuticle: absent (0), present (1).
 - 12 Eyes comprising calcite prisms: absent (0), present (1).
 - 13 Cephalon matching pygidium closely in proportions and outline: yes (1), no (0).
 - 14 Dorsal facial sutures: absent (0), opisthoparian (1), proparian (2).
 - 15 Palpebro-ocular ridges: absent (0), present (1).
 - 16 Genal spines: present (0), absent (1). Note: genal spines are secondarily developed on some Agnostina (e.g. *Triplagnostus*); these may or may not be homologous with those on other trilobites, but are present on neither of the taxa coded here.
 - 17 Rostral plate: absent (0), present (1), [secondarily lost (2)].
 - 18 Occipital width: exceeds width of glabella in front (1), does not exceed (0). Note: the agnostoid occipital ring is understood to include the triangular lateral lobes.
 - 19 Cephalic shield long, sagittal length equal to, or exceeding transverse width (which is often anterior to posterior cephalic margin) (1), cephalic shield wider than long, and with maximum width at posterior margin (0). (Note: the progenetic *Olenelloides* provides one exception.)
 - 20 Cephalic border: 'rolled' (1), flattened (2), border absent (0).
 - 21 Connective sutures: present (1), absent (0).
 - 22 Pygidial length: exceeding cephalic (1), less than or subequal (0).
-

with a tree length of 149. This cladogram uses the characters and coding discussed at length in Wills *et al.* (1994), to which the reader is referred for details. In the present context there is no particular purpose in including *all* the other Burgess type arthropods, and this cladogram includes only two arachnids, including a limuloid (*Tachypleus*), five arthropods with crustacean-like bodyplans (the clade *Galathea* to *Speleonectes*); the lobopods, *Aysheaia* and *Peripatus*, and an annelid are outgroups. With a consistency index (excluding uninformative characters) of 0.51 this tree is better supported than the more inclusive trees published previously (Briggs *et al.* 1992). The trilobite clade is quite well defined. The Burgess Shale arthropod *Emeraldella* occupies the position as sister taxon to the Trilobita. Synamorphies are listed in the legend to Text-figure 5.

This treatment gives *Naraoia* as the sister group of higher trilobites, a clade comprising *Agnostus* and *Olenoides*. It would be possible, if one wished, to exclude *Naraoia* from the trilobites by appropriate definition (a view like that of Ramsköld and Edgecombe 1991) although this would not be our recommendation. The naraoiids are consistently associated with other arthropods regarded as trilobites in all other analyses (e.g. Briggs *et al.* 1992) and it seems to us unwise to proliferate taxa at the highest level. Furthermore the Trilobita, including naraoiids, comprise a clade equivalent to other clades conventionally regarded as classes or subphyla (Arachnida, for example).

The question of how agnostids relate to Eodiscina cannot be resolved by this kind of analysis, because the latter are not known from specimens showing ventral limb morphology. Are agnostid peculiarities a product of progenesis? A similar case among Crustacea is the difficulty of recognizing the sister group of Copepoda (Schram 1986). To examine this problem in an appropriate way we

next analyse the agnostids in relation to other Cambrian trilobites, including naraoids, olenellids, redlichiids and eodiscoids, which have been cited as relevant to the 'agnostid problem'.

Walossek and Müller (1990) noted resemblances between *Agnostus* and what they termed 'stem group Crustacea' from the Upper Cambrian *Orsten* of Sweden. The most impressive of these are apparent limb homologies between *Hemmingsmoenia* and *Agnostus*; the former also had a hypostome. However, *Hemmingsmoenia* is a minute arthropod, with an enlarged dorsal shield, and its position within the 'stem arthropod' complex is at least as difficult to decide as that of agnostids. It does not have a pygidium, neither are its eyes included in the dorsal shield, nor is its carapace calcified. Five pairs of cephalic limbs are more than is characteristic of trilobites, or *Agnostus*. It is interesting to note the resemblance between the shield of *Hemmingsmoenia* and the minute, phosphatized carapace regarded as a 'pre-protaspis' (phaselus) trilobite larva by Fortey and Morris (1978). It is possible that the minute *Hemmingsmoenia*, too, is progenetic, and that the limb resemblances between it and agnostids betray a similar ontogenetic ancestry.

Exoskeletal characters and the agnostid problem

In order to examine the relationships of agnostids using a wider variety of relevant trilobites, it is a requirement that characters of the exoskeleton are used, because several of the trilobites concerned are not known with appendages preserved. Fortey (1990) considered this problem, using his own judgement on relevant synapomorphies, and without the inclusion of naraoids in the analysis. Here we analyse the problem using a computer based parsimony analysis (PAUP vs. 3.1). Olenellids are accepted as trilobites (Fortey and Whittington 1989; Ramsköld and Edgecombe 1991). A limuloid is the outgroup. The new naraoid, *Soomaspis*, is included, not least to establish that our view of its inclusion within the same clade as *Naraoia* is justified. Characters used are shown in Table 1 and their coding in Table 2.

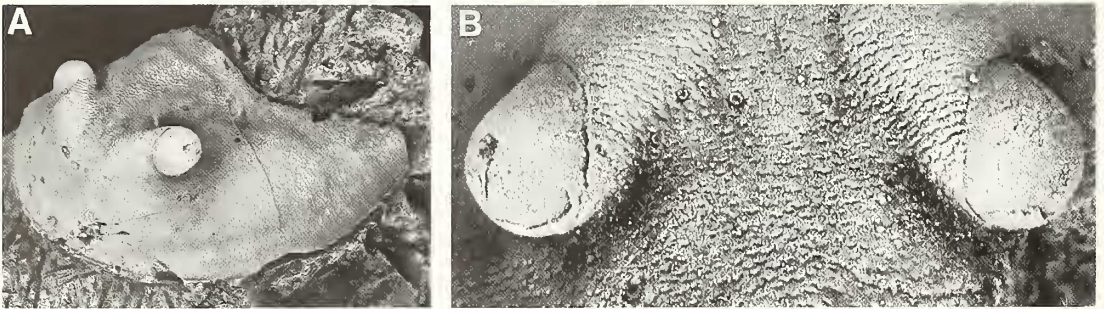
TABLE 2. Coding of characters given in Table 1 for the cladogram, Text-figure 7. See text for further discussion.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Naraoia</i>	0	2	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	?	0	0	0	1
<i>Soomaspis</i>	0	2	0	0	1	0	0	0	1	1	0	0	0	0	0	1	1	?	0	0	1	1
<i>Agnostus</i>	1	1	2	1	1	1	0	0	1	1	1	0	1	0	0	1	0	1	1	1	0	0
<i>Pagetia</i>	1	1	1	1	1	1	0	1	1	0	1	1	1	2	1	1	0	1	1	1	0	0
<i>Tril (Olenoides)</i>	1	0	1	0	1	0	1	1	1	0	1	1	0	1	1	0	1	0	0	2	1	0
<i>Olenellus</i>	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	1	0	0	2	0	0
<i>Tachypleus</i>	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	?	0	0	0	0

It should be noted that there are some differences in character interpretation between Fortey and Whittington (1989) and Ramsköld and Edgecombe (1991). The former were concerned primarily with the place of olenelloids (then being studied by Whittington, see Whittington 1989) within the Trilobita, as opposed to claims (e.g. Lauterbach 1983) that some olenellids were more closely related to limuloids and other arachnoids than to Trilobita *sensu stricto*. *Naraoia* was specifically omitted from the discussion, an omission that Ramsköld and Edgecombe (1991) regarded as 'unfortunate'. In fact, one of us was already addressing the problem of the place of naraoids (and agnostids) in a different publication (Briggs and Fortey 1989) as the first of several analyses using a wider spectrum of arthropods. These studies dealt with problems concerning outgroup definitions raised by Ramsköld and Edgecombe (see Smith 1994). However, some of the characters used by Fortey and Whittington are used again herein, and the comments of Ramsköld and Edgecombe need brief reference, especially where there are factual errors. The following comments also encompass points made by Shergold (1991).

1. Pygidium. The possession of a pygidium comprising two or more fused segments was regarded by Fortey and Whittington (1989) as a typical trilobite character. Ramsköld and Edgecombe (1991) stated that the 'pygidium' of *Olenellus* had only one segment (regarded as a possible autapomorphy of Olenellidae). However, Whittington (1989, p. 119) described the pygidium of the type species of *Olenellus*, *O. thomsoni* – the reference point for discussions of olenellid anatomy – as including more than one segment, because 'inter-ring furrows' were recognized, and mentioned in his description. It is widely recognized that there *are* examples in undoubted Trilobita where the release of thoracic segments into the thorax proceeds to the point where only a single posterior plate remains (e.g. *Celmus*, see Bruton 1983), but this is secondary. But this is not true of *O. thomsoni*, even if it may apply to other olenellids.

2. Calcified lens structure. The trilobite eye is uniquely constructed. Fortey and Whittington scored the eye as a character separate from calcification of the cuticle, a view which was criticized by Ramsköld and Edgecombe (1991) on the grounds that it was 'unknown whether [eye structure] can be treated as an independent apomorphic character'. They state that 'the mineralogy and optical axis are two characters that are obligately coupled in trilobites'. However, the prismatic structure of the calcified corneal surface differs fundamentally from laminated structure elsewhere in the cuticle (Clarkson 1975). Furthermore, because primitive trilobites have a circum-ocular suture, there was really no obligation for the corneal surface to behave in the same way as the rest of the cuticle. An example of an undescribed aglaspid with calcified cuticle but apparently phosphatic corneal surface (Text-fig. 6) illustrates this decoupling. It seems rather unlikely to us that



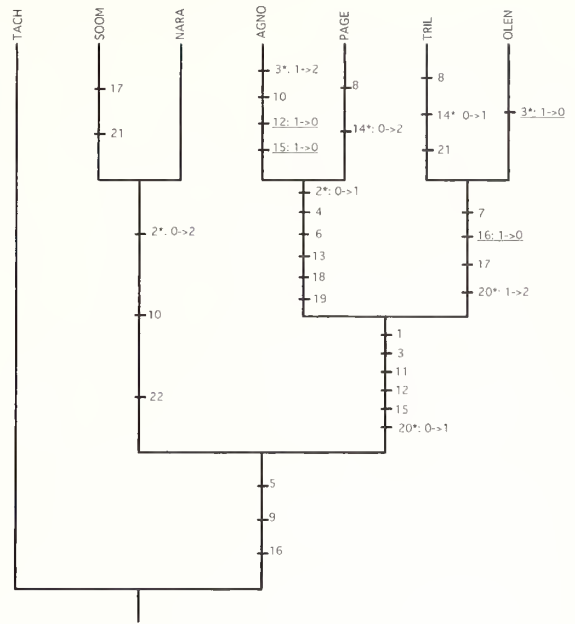
TEXT-FIG. 6. Eye of an undescribed Chinese Silurian aglaspid showing difference in composition from calcareous cuticle. The eye is phosphatic, but this may be after a different original matrix. A, anterior oblique view of prosoma; $\times 4$; B, detail of eyes, dorsal view; $\times 8$. (Photographs supplied by Dr Derek J. Siveter).

calcification of the cuticle *and* the specialized structure of the corneal surface could have been achieved as a single mutation. Nor do other calcified arthropods (ostracodes, decapods) solve their optical problems in the same fashion as trilobites. Fortey and Whittington (1989) were probably entitled to regard optical and cuticular characters separately.

3. Rostral plate. Detailed comments on the importance of the rostral plate were given by Fortey (1990). Evidence for a rostral plate in *Soomaspis* is discussed above, but for other naraoiids the evidence is equivocal. The *Naraoia* species illustrated by Zhang and Hou (1985, pl. 1) clearly shows the hypostome in conterminant attachment mode, but it is hard to assess whether the rostral plate is a separate structure, or whether the doublure is in continuity with the dorsal surface. Note that Ramsköld and Edgecombe (1991, fig. 1), show 'rostral plate' as a synapomorphy of Eodiscoidea and 'more derived trilobites', whereas the former group apparently lacks such a plate (Jell 1975, pl. 1, fig. 1; see also Fortey 1990, text-fig. 13).

4. Hypostome. Fortey and Whittington (1989) cited the hypostome, together with anterior wings that articulate against the fossulae in the axial furrows, as a trilobite character. It is a complex structure, which might have been 'broken up' into more than one character, but does indeed seem

TEXT-FIG. 7. Cladistic analysis of relationships of agnostids to naraoids and other trilobites based on the character matrix given in Table 2. Characters listed in Table 1. This version does not assume that agnostids and eodiscids had an *Olenellus*-like rostral plate which was secondarily lost. Tree length = 34 steps; Consistency Index = 0.77. PAUP vs. 3.1, on Mackintosh. On this and the following figure character reversals are indicated by asterisks, and changes in multi-state characters are underlined.



to be characteristic of an enormous range of trilobites (Whittington 1988a, 1988b; Fortey 1990). Ramsköld and Edgecombe (1991) cast doubt on whether the trilobite and agnostid hypostome were truly homologous, basing their arguments mostly on *Agnostus* (Müller and Walossek 1987). They may have been unaware that Robison (1988, fig. 9) described a hypostome of *Oidalagnostus trispinifer*, complete with wings, which is similar to that of *Pagetia* (Eodiscina) (see Jell 1975), and also like that of many ptychopariids. The hypostome of *Naraoia* has been figured by Zhang and Hou (1985, pl. 1). It would certainly be good to know more about hypostome-like structures of likely trilobite sister taxa, as Ramsköld and Edgecombe say, and this will serve to focus future work. However, it does seem to go against common sense to assume that a complex structure like the hypostome evolved entirely in parallel between pagetiids and other trilobites on the one hand, and agnostids on the other.

5. Larval characteristics. Much has been made by Shergold (1991) of the fact that pagetiids (Eodiscoidea) had calcified protaspis larvae (see also Zhang 1989). Neither agnostids nor olenellids had calcified protaspides, so far as is known. This character, in particular, is cited as evidence that eodiscoids and agnostids had separate phylogenetic origins, the former within a clade of 'higher' trilobites, the latter with a separate trilobite-like ancestor within that grade of organization at which protaspides had not yet calcified. The results of our analysis indicate an alternative hypothesis, which includes pagetiids and agnostids as sister groups, which then supposes the non-calcification of the agnostid protaspis to be secondary, perhaps another consequence of progenesis.

The three different hypotheses for agnostid relationships have different consequences for future discoveries. Shergold's (1991) view predicts that no calcified agnostid protaspis shall ever be discovered, nor any eodiscoid discovered without one. Zhang *et al.*'s (1980) polyphyletic view predicts that calcification was lost more than once, hence, presumably, early agnostids might still retain a calcified protaspis, and/or the appropriate eodiscoid ancestor may already have lost it. The hypothesis supported here shows that no eodiscoid should be without a calcified protaspis, but it remains possible that not all the autapomorphies supporting the agnostid clade were acquired at the same time, and hence that a primitive agnostid (likely to be stratigraphically lower, in the Lower Cambrian) still retained a calcified earliest growth state. Perhaps the potential resolution of these